Continuous bite monitoring: a method to assess the foraging dynamics of herbivores in natural grazing conditions

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Abstract. Accurate estimates of bite mass and variations in the short-term intake rate of grazing herbivores has been historically considered as a fundamental methodological difficulty, a difficulty that increases with the complexity of the feeding environment. Improving these methodologies will help understand foraging behaviours in natural grazing conditions, where habitat structure and interactions among different forages influence feeding decisions and patterns. During the past 30 years, we have been developing the ‘continuous bite-monitoring’ method, an observational method that allows continuous assessment of foraging behaviours, including bite mass, instantaneous intake rate and food selection, in simple to complex feeding environments. The centrepiece of the method is a ‘bite-coding grid’ where bites are categorised by structural attributes of the forage to reflect differences in bite masses. Over the years, we have been using this method with goats, sheep, llamas and cattle across a range of different habitats. After reviewing the development of the method, we detail its planning and execution in the field. We illustrate the method with a study from southern Brazilian native Pampa grassland, showing how changes in the forages consumed by heifers strongly affect short-term intake rate during meals. Finally, we emphasise the importance of studying animals grazing in their natural environments to first identify the relevant processes that can later be tested in controlled experiments.

Additional keywords: bite mass, direct observation, foraging strategy, intake rate, rangelands.

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Introduction

A central issue in grazing studies is to understand how vegetation structure and composition influence the rate at which animals ingest plant material and thereby nutrients. On sown swards, this relationship is at the core of management practices (Hodgson 1985; Parsons and Chapman 2000), whereas in more complex grazing contexts, such as natural grasslands and scrublands, it is essential for testing the validity of foraging models (Stephens and Krebs 1986; Farnsworth and Illius 1998; Bergman et al. 2001). However, measuring short-term intake rate by herbivores, and how local differences in vegetation structure and composition affect this rate, has long been a major methodological issue because of the difficulty to obtain reliable estimates of individual bite mass (BM) (Van Dyne et al. 1980; Gordon 1995; Mayes and Dove 2000). Many studies have overcome this difficulty through the use of simple feeding environments, such as sowed monoculture swards (Allden and Whittaker 1970) or hand-constructed micro-sward boards (Black and Kenney 1984). Their objective was to provide a relatively homogeneous canopy where average bite properties (BM, bite rate, bite dimensions) over a limited grazing period (generally less than 1 h) could be considered as representative of the functional link between the structural properties of the sward canopy (sward surface height, bulk and tiller density, herbage mass) and bite formation. The average BM was determined by weighing the micro-sward boards before and after the animal fed (Ungar et al. 1991; Laca et al. 1992a) or, in the case of sowed monoculture swards, by either using oesophageal-fistulated (Stobbs 1973) or rumen-cannulated animals (Gregorini et al. 2009), or by double weighing the animal before and after the grazing session (Penning and Hooper 1985; Gibb et al. 1997). While these methods improved understanding of the plant–animal interface in a simple and controlled feeding environment, understanding how vegetation properties influence forage intake and food selection in more complex feeding environments remains challenging.

Extending the results from short-duration, controlled grazing experiments to natural grazing conditions, on either monoculture pastures or diversified grasslands, is difficult because most protocols interfere with various components of the animals’ living environment. Such components include the daily patterns of activity (Gregorini et al. 2008; Gregorini 2012), the
social environment (Arnold 1985) or the comfort of evolving in a familiar habitat (Burritt and Provenza 1997; Bailey and Provenza 2008), all being components that influence foraging decisions. The challenge is even greater in complex feeding environments, where interactions between different plant species or plant parts can greatly influence the animal’s foraging decision (Belovsky 1984; Provenza 2006; Provenza et al. 2007; Lyman et al. 2011), intake rate (Courant and Fortin 2010) or daily intake amount (Agrell et al. 2006; Cortes et al. 2007; Meuret and Provenza 2015). Hence, the methods that allow researchers to assess foraging components in natural grazing conditions are important. Various techniques exist for estimating daily intake on complex pastures (Dove and Mayes 1991; Penning 2004), but they require daily manipulation of the animals. Over shorter time periods (few minutes to 1 h), double weighing of the animals or oesophageal fistulation can be used, but these techniques are invasive and not always practicable on rangeland. Nevertheless, these methods can capture only the average BM, bite rate and intake rate over entire grazing sequences or days. They cannot inform researchers about variations of these variables as a function of local differences in the sward structure and composition.

During the past 30 years, we have been developing and improving a method based on the direct observation of foraging behaviours of herbivores maintained in their natural grazing conditions. The method allows continuous estimation of BM, time per bite, instantaneous intake rate, selection of plant species and plant parts in relation to local vegetation properties, as well as their dynamics along entire feeding bouts and days, in either simple or complex feeding environments. In this paper, we present the origin, rationale and fundamental elements of the continuous bite-monitoring method, and discuss its application and value relative to other techniques.

The ‘continuous bite-monitoring’ method
Origins and development

Direct observations have been used to assess the feeding habits and diet composition of free-ranging herbivores for more than 80 years (Dixon 1934; Doran 1943). In most of these studies, diet composition was estimated by the percentage of time the animal spent feeding on different plant species, and BM was generally ignored. So as to account for variations in the handling times of different forages, Reppert (1960) counted the number of bites taken from each plant rather than the time spent feeding on them. Differences in BM were roughly estimated through three or four bite-size categories. To improve estimations of BM, Free et al. (1971) used oesophageal-fistulated animals. But estruses generally contained material from bites of different size and taken from different plant species, making it difficult to link BM to a particular plant species or structure. Hand-plucking (Halls 1954), another technique to estimate BM, consists of simulating bites by manually collecting plant tissues as cropped by the animal. Hand-plucking causes minimal disturbance to the animal and allows for the estimation of the mass of single bites instead of average values of BM over a duration determined by the experimental procedure. Through the years, the combination of the bite-count and hand-plucking techniques has been used to estimate short-term intake rates and diet composition of a wide range of wild ungulates on rangelands (e.g. Collins et al. 1978; Collins and Urness 1983; Renecker and Hudson 1985; Hudson and Frank 1987). This approach seemed particularly promising in a complex feeding environment where the interest was to link the short-term intake rate of forage to local vegetation properties and to their variations in space and time.

Inspired by these above-mentioned studies with wild ungulates, Meuret et al. (1985, 1986) used the bite-count and hand-plucking methods to estimate diet composition and daily intake levels of dairy goats herded in Mediterranean woodlands. As the objective was to assess daily intake and relate it to milk production level, authors wanted to minimise impacts on herding activities, grazing habits and feeding choices. Meuret et al. (1985) also used the chromic oxide method on five individuals so as to validate estimations of daily intake made through the bite-count method. After correction for in vivo digestibility of woodland forages in dairy goats usually grazed in this kind of environment (Meuret 1988), the two methods gave very similar results. To validate mean BM estimations of the most consumed plant species, Meuret et al. (1985) also double-weighed freshly cut branches offered to an animal browsing a natural stand of the same species. As for studies conducted with herbage species, the authors observed that BM was better explained by foliage structure and density than by plant species. For example, the coefficient of variation for BM from white oak (Quercus pubescens Willd.) reached 30%. As a result, Meuret et al. (1985) considered that the mean BM for this species could lead to errors of 15% in the estimation of daily intake. Meuret et al. (1985) concluded that when using the bite-count method, an estimation of average BM per plant species was unsatisfactory and that BM estimations must also integrate structural attributes of the forage. In a subsequent study on the foraging behaviour of goats and llamas on a Mediterranean scrubland, Dumont and Meuret (1993) defined three to eight types of bite per shrub species (see also Dumont et al. 1995). Using these species-specific bite types, they recorded from dawn to dusk all the bites taken by selected individuals foraging within their group of conspecifics. Mean BM of each bite type was then estimated by hand-plucking. Dumont and Meuret (1993) observed that some forages (e.g. Juniperus oxycedrus L.), when grazed over several minutes, allowed the animals to significantly increase their instantaneous intake rate through the consumption of massive bites (up to 0.02 g DM/bite per kg liveweight0.75). This observation would not have been possible with average values of BM or intake rate. Indeed, the result of these accelerations was not an increase in the level of daily intake. Rather, local accelerations allowed the animal to spend more time in exploring the pasture, eating small, highly nutritious plants or ruminating less digestible forages (Meuret 1997). The continuous bite-monitoring method not only allowed the authors to estimate levels of daily intake consistent with the literature (Dumont et al. 1995), but it also gave valuable information on the grazing strategy used by the animals to reach these levels of intake in a complex pasture.

Still, the need to define different types of bite for each plant species rapidly appeared as a limiting factor for using the continuous bite-monitoring method in diverse plant communities. To improve the effectiveness of this method in a
complex environment, and following the hypothesis that the local forage structure was a principal determinant of BM, Agreil and Meuret (2004) classified all possible feeding bites independently of the plant species. The resulting ‘bite coding grid,’ first developed for small ruminants grazing on French rangelands, defined a series of ‘bite categories’ on the basis of the nature and structure of the selected tissues (Agreil and Meuret 2004; Agreil et al. 2005, 2006). Other bite-coding grids were subsequently developed on the same principle for heifers grazing high mountain pasture in the French Alps (Agreil and Meuret 2008) and sheep and goats grazing in a deciduous tropical forest of Mexico (González-Pech et al. 2014). Bonnet et al. (2011) tested in South Africa the accuracy of this system of classification to estimate BM and short-term intake rate through hand-plucking. They offered freshly dug patches of natural grassland in the form of micro-sward boards to cattle and goats and compared BM estimates from hand-plucking and double-weighing of the boards. After just a few days training, the four observers reached levels of accuracies from 80% to 94% for BM and, because BM estimations were not biased, higher than 95% for short-term intake rate. More recently, for a study of the grazing behaviour of heifers in South Brazilian native Pampa grasslands, bite depth was added as an additional factor in the coding grid. We describe this last study in more detail below, to provide an example of the insights that can be gained from the continuous bite-monitoring method.

Accounting for the natural living and feeding environment of the animals

An important concern while developing the continuous bite-monitoring method was to minimise the impact of the study on the animals’ natural living and feeding habits. First, most domestic herbivores are born and live in social groups, which have structure, integrity and particular habits. In domestic livestock, group cohesion and hierarchy emerge from animals’ inter-individual affinities, as matrilineal groups are generally not allowed to form (Stamps and Groothuis 2010; Shaw et al. 2005, 2006). Other bite-coding protocols (i.e. the bite-coding grid) as described below. The basis of this mutual familiarisation procedure came from 30 years of constant interaction with experienced livestock farmers and herders who had expert knowledge of their animals’ attitudes and behaviour (Meuret and Provenza 2015). The procedure progressively has been adjusted following their advice, until they commented on the lack of detectable impact of the observer on individual or group behaviour. Duration of the familiarisation depends on the animal species under study, group size, habitat as well as the nature of previous contacts the animals have had with humans. It can take from 3 to 5 days with small or medium-sized groups of closely herded dairy animals, and up to 20–30 days with large herds of recently dried or pregnant animals grazing freely in large paddocks.

The first step of the mutual familiarisation procedure is to make contact with the herd or flock. Effective familiarisation requires that the animals perceive the observer as different from farmers or herdsmen. General rules are as follows: (1) wear clothes that are different from those of farmers or herdsmen; (2) avoid direct contact with the animals at the barn or within a sorting pen and instead organise the first encounter on the grazing land at a time of the day farmers and herdsmen usually do not come; (3) come first when animals are satiated, calm, comfortable and grouped in a familiar place, which typically can be undertaken when animals are lying down in a mid-day resting place or in the night pen; (4) remain easily visible at a distance, and take the necessary time (hours if necessary) to wait until all of the animals are calm; (5) talk to the animals to help them identify the voice of the observer; and (6) try to reduce progressively
the distance to the group, while checking whether any animals are disturbed. This first contact period with the group, which can take several consecutive days, ends when no single animal appears disturbed by the presence of the observer at a distance of ~0.5 m.

The second step of the familiarisation procedure is to identify potential focal individuals and familiarise them with the close and continuous presence of the observer. Focal individuals should neither be leaders nor particularly fearful (i.e. by systematically stopping their activity and maintaining a certain distance from the observer) or demanding (i.e. by stopping their activity to interact with the observer). From our experience, most individuals can be observed after proper familiarisation. While the focal individual is grazing, the observer remains visible on its side, sometime speaking, and always avoiding impeding its contact with conspecífics. Following the focal individual for several days, the observer progressively reduces his distance to it.

By the end of the familiarisation procedure, the observer should be able to move around the focal individuals at a distance of ~0.5–2 m without any detectable changes in individual and group behaviour. By that time, the focal individual should start to occasionally push the observer with its head (sheep or goat), or move its head as if it wants to do so (cattle), because the observer stands in its line of movement. Although this situation should be avoided during data acquisition, it gives a clear indication that the animal considers the observer no more worrying than any conspecific. As a specialist in animal behavioural studies wrote about this mutual familiarisation procedure, ‘To be sure that you’re not disturbing the animal: just let him tell you!’ (Despret 2009).

Design of the bite-coding grid

The bite-coding grid allows the observer to record in real time a detailed description of all bites taken by the animal. The principle is to define a limited number of bite categories (BC) (ideally between 20 and 45, depending on the structural diversity of the forage) on the basis of the following four distinct criteria: (1) nature and position of the selected plant parts (within the plant but also within the plant community); (2) structural attributes of the tissues (three-dimensional architecture, density); (3) handling and severing behaviour of the animal (e.g. tissues being regrouped with the tongue, cleanly cropped with the teeth or broken at their base); and (4) expected nutritional value of the bite. Plant species should not be used as distinctive criteria, except when they possess a very distinctive tissue structure. With grass species, bite depth is an important determinant of BM. Rather than creating new BC for each bite depth, a number (in cm) corresponding to an evaluation of bite depth or sward height can easily be added to the BC code during data acquisition. While closely watching the animal, the observer will combine similar bites into BC, each BC being illustrated by a pictogram of the ‘ideal bite’ (Fig. 1). The number of BC will depend on the balance between having a coding grid sufficiently detailed to adequately describe the feeding behaviour of the animal, but not so detailed that the observer hesitates to attribute bites to one or another BC. Effectiveness of the coding grid will depend on this balance and must be tested before its utilisation. Equipped with a first version of the grid, the observer should follow an individual and try to code as many bites as possible. There are three possible outcomes from this test. First, the observer might find it difficult to choose between two BCs. In this case, the observer needs to consider grouping these BCs, or else, defining them better. Second, the observer may find that one BC is too broadly defined and decide to divide it in two subcategories. Finally, a completely unexpected type of bite can be observed, forcing the observer to add a new BC to the coding grid. When different observers are involved, it is recommended that they work together on the design and refinement of the coding grid, so as to ensure that bites are coded in the same way.

Training of the observers

Training is an essential part of the method. Monitoring feeding in real time requires being able to identify BCs as well as the plant species almost reflexively. For that reason, training needs to be progressive, adding additional levels of information once the previous one is mastered. While observing the animal for several hours, the observer first trains himself to identify bites with respect to the BC of the grid. Second, the observer must practise dictating in real time the BC codes corresponding to observed bites. Finally, the observer can add the identity of each plant species. Training can be considered completed only after the observer is able to encode every single bite without hesitation.

Protocol: data acquisition

Remaining alongside the focal individual and always visible, the observer makes sure he has a good view of the animal’s mouth and selected plant parts. When the animal is eating, the observer encodes each bite by juxtaposing the BC code, the plant species code and eventually the bite depth (or sward height). To facilitate the encoding process, plant species are recorded only when the animal selects a new plant species. Specific codes can also be used when the animal moves its front legs (allowing identification of the feeding stations) and other behaviours such as drinking, resting or ruminating. The use of a microphone and a digital recorder is recommended, as it allows the observer to concentrate on animal behaviour. Later, recordings of feeding sequences are transcribed using specific software (e.g. JWatcher®, http://www.jwatcher.ucla.edu/, verified 10 December 2014; The Observer, Noldus Information Technology®, The Netherlands). Depending on the scientific question, observations can be made from minutes to hours, or continuously over the entire day. When possible, multiple animals should be observed to ensure validity of the data. This can be done either simultaneously by several observers, or on successive days with a sufficient number of repetitions per individual. When working with large herds or flocks, consistency in the patterns of activity and diet quality between focal individuals and the rest of the group can be assessed through scan sampling and faecal near-infrared reflectance spectroscopy (Lyons and Stuth 1992), respectively.

Bite mass and its nutritional value are estimated by hand-plucking plant tissues corresponding to each BC from each plant species contributing to the diet. On non-observational days, the
observer stays close to the animals, observes their feeding behaviour and then plucks tissues to simulate the bites, using, if possible, the same plants as selected by the animals. This ensures that simulated bites are as close as possible to the real ones. The more frequently the BC is observed in the diet, the larger the number of samples. Alternatively, samples from non-selected plant parts or plant individuals can also be collected and compared with samples from selected plant parts if, for
example, the scientific question includes determining the selective behaviour of the animal. Samples are then dried and weighed to determine BM and for chemical analyses.

An example of a recent application of the method

A bite-coding grid for heifers grazed on Brazilian pampa grassland

In 2012, we conducted a study on the grazing behaviour of 2-year-old heifers grazed year-round on native Brazilian pampa grassland. The local plant community is extremely diverse (>170 native plant species from 35 families and up to 45 species per m²), with both C3 and C4 grasses and forbs, but without shrubs or trees (Fischer 2013). The resulting feeding environment is particularly complex, with a high number of plant structural types and species intermixed in both horizontal and vertical dimensions (Fig. 2). Heifers grazed in groups of 4–10 individuals, distributed in 10 paddocks 4–5.5 ha in size. Except for adjustments in stocking rate, there was no other human intervention in the study area (see Da Trindade et al. 2012 for a full description of the study protocol).

The bite-coding grid we designed for this study (Fig. 1) distinguished bites taken from short sward, tussocks and forbs, as they involved fundamentally different forage structure. For example, in the short-sward group, the BC ‘mix’ corresponds to bites made on short lawn-sward formations, whereas the BC ‘B’ represents a bite made from short grass species that have grown taller due to the relative protection of an adjacent tussock. From the tussock group, BC ‘F’ represents a bite taken from the top of a tussock, BC ‘C’ the grazing of an already intensively cropped tussock and the BC ‘S’ the prolonged gathering of a small number of leaves (≤3) from an individual grass that has grown through a larger plant. Because of the unique structure of Eryngium horridum Malme (Apiaceae), six BCs were created for this plant. In addition to the 32 BCs of the coding grid, we used some modifiers to reduce the number of BCs. For example, we added the code ‘i’ after any BC from tussocks when the bite was composed of a small number of leaves. We also added the code ‘P’ when the plant material was pulled and thus broken at its base rather than cropped with the teeth (see Fig. 1; ‘pulled bites’). For short-sward BC, we also recorded sward height, whereas we used bite depth for BC from among the tussocks.

Exploring the dynamics of heifer foraging behaviour

To illustrate the method, we present data from a half-day grazing sequence of a 270-kg heifer observed in spring 2012 (Fig. 3). During that morning, the heifer ate two meals separated by a short period of rumination. Grazing activity stopped ~1100 hours when the heifer rested and started to ruminate. Short-term ingestive behaviour was highly variable, as illustrated by the wide range in bite masses at any one time (black points), resulting in strong variations of the instantaneous intake rate (grey line). Interestingly, we did not notice any inflexion of the intake rate at the end of meals, as illustrated by the slope of cumulative intake (black line). Inflexion of the cumulative intake generally occurs in the case of a single forage given to a ruminant at the trough or as a monoculture (Suzuki et al. 1973; Baumont et al. 1989). Orr et al. (2001) found that this inflexion results from an increasing frequency and duration of the non-feeding bouts and reflects an increasing level of satiety. In the case of the heifers we observed, non-feeding bouts were nearly absent throughout the meals (Fig. 3). Different hypotheses can explain this result. The wide variety of forages consumed (more than 30 different plant species in this case) could have prevented a decrease in the animal’s motivation to eat by the end of the meal, as observed for herded animals (Meuret and Provenza 2015; Provenza et al. 2015). Alternatively, the animal could have ended its meal for an external reason (e.g. heat) before being satiated (see also Forbes and Gregorini 2015).

In-depth analysis of the grazing sequence (Fig. 3) gives information on the link between the forage on offer, the

Fig. 3. Grazing sequence during a morning for a 2-year-old heifer grazing freely in a 4.2-ha paddock of native Pampa grassland. Black points represent bite-mass estimates (g DM/bite) all along the sequence. The black line represents the cumulative intake (g DM). The grey line represents the dynamic of instantaneous intake rate (g DM/min, calculated by summing the estimated mass of all observed bites over 1-min periods). Drinking (Dr) and ruminating (Ru) periods are indicated.
heifer’s selective behaviour and its ingestive dynamic. Referring to the coding grid (Fig. 1), bites from the first meal (0545 hours to 0810 hours) mainly consisted of BCs from the short-sward group (72%, with a mean sward height of 4.0 cm), the rest constituted of bites from small (‘T’, 5%), grazed (‘C’ and ‘K’, 9%) and tall tussocks (‘F’ and ‘S’, 8%). Interestingly, the higher intake rate observed between 0630 hours and 0700 hours than in the previous period (from 6.7 to 8.0 g DM/min) was not due to an increase in the mean bite mass, which remained constant at ~0.17 g DM (±0.9 s.d.), but to an increase in bite rate, from 39 to 48 bites/min. This increase in bite rate was the result of a higher foraging efficiency (the proportion of non-feeding steps decreased from 25% to 2% and the number of bites per step increased from 5.8 to 13.5; Searle et al. 2007). In addition, the proportion of BC ‘S’ in the diet decreased (from 8.7% to 5%). BC ‘S’ had a relatively low bite mass (0.13 g DM ± 0.05 s.d.) and required long gathering time (2 s ± 1.6 s.d.). These results emphasise how weak the link between bite mass and bite rate can be in complex pastures. In such pastures, the density of preferred bites is highly variable in space (among feeding patches) and time (during the meal), which strongly affect feeding-station behaviour and bite rate through selection. Moreover, small bites often require long gathering time (e.g. BCs ‘S’ and ‘F’ in Fig. 1), whereas large bites can be cropped rapidly, depending of the forage structure (Agreil and Meuret 2004). These processes, by affecting selection, bite rate and instantaneous intake rate, can be of primary importance in shaping the meal dynamic of herbivore foraging in complex pastures.

During the second meal (0900 hours to 1100 hours, Fig. 3), the animal remained in a flooded area for the first hour, mostly grazing *Luziola peruviana* Juss., a highly palatable grass that grows on top of the water but requires high gathering time and permits only small bites (0.12 ± 0.03 g DM). During the second hour, the heifer moved out of the water to another area where it diversified its intake, with bites ranging from 0.08 to 1.0 g DM grazed from >15 plant species from short swards (76% of total bites), small tussocks (9%) and grazed tussocks (13%). This time, the strong increase in the intake rate relative to the previous hour (from 7.1 to 10.4 g DM/min) was not due to higher foraging efficiency (non-feeding steps remained at ~18%), but to an increase in both bite mass (from 0.14 ± 0.04 to 0.20 ± 0.08 g DM) and bite rate (from 47 to 54 bites/min). This was due to larger bites taken on short sward (0.17 ± 0.04 g DM), a higher proportion of bites taken from small and grazed tussocks that allow massive bites (BC ‘T’, ‘C’ and ‘K’ of the coding grid, Fig. 1, BM ranging from 0.19 to 0.7 g DM), and an absence of the time-consuming BC ‘S’. Once again, these results emphasise that bite mass and bite rate are poorly linked in complex pastures and that the animal can increase its instantaneous intake rate by temporarily increasing both bite mass and bite rate (see also Meuret 1997; Meuret et al. 2013). Depending on the grazing patches and forage it selects, an animal has the ability to modify its short-term intake rate of dry matter and nutrients during the meal. In the example of Fig. 3, the heifer concentrated its foraging on a highly palatable and nutritive plant species during the first hour of the second meal. During the second hour, it changed its foraging pattern and achieved the highest intake rate of DM of the morning, possibly in an attempt to compensate for the very low intake it achieved during the previous hour.

**Discussion**

The range of methods available for data acquisition determines not only our ability to answer scientific questions, but also our capacity to formulate them (Callon et al. 1986; Legay 1997). The use of ‘laboratory-type’ experiments in grazing studies, based on a ‘laboratory model’ approach (Hatchuel 2000), is plainly justified when the scientific question is to understand a particular process while isolating it from the large number of other processes that occur in natural, and always complex, systems. This complexity cannot, however, be ignored and the use of a ‘field-model’ approach (Hatchuel 2000; Hubert et al. 2008) becomes necessary. Direct observation techniques have long been used for studying the foraging behaviour of herbivores in their natural environment. Being mostly descriptive, these studies raised criticisms about their subjectivity and their inability to assess accurate levels of forage intake (e.g. Holechek et al. 1982; Mayes and Dove 2000). However, being non-invasive, less costly, flexible and able to assess a great deal of details (e.g. bite structure, handling time, cropping behaviour, plant species and plant parts consumed), they can be used in nearly any kind of environment. Working mostly on the foraging behaviour of herded or free-ranging herbivores in complex feeding environments such as woodlands, scrublands, and highly diversified grasslands, we have tried to improve the accuracy of some direct observation techniques for estimating bite mass, intake rate and the link between these variables and the nature and structure of selected plant species and tissues.

The advantage of the continuous bite-monitoring method over other existing techniques is that it gives access to key foraging processes (i.e. bite mass, bite rate, intake rate and feeding-station behaviour), as well as their dynamics during the meal, in relation to the nature, structure and location of the selected food items. To our knowledge, no other method can do this. The method is also extremely flexible and can be adjusted to address a large range of scientific questions. Foraging processes can be assessed repeatedly over a few minutes, hours, or be collected continuously over entire daylight periods. The method can be used in either simple or complex feeding environments composed of hundreds of plants. Classification of bites in the coding grid can be adapted to focus more on bite mass, plant parts selected or position of the selected plant within the plant community. Nevertheless, some aspects of the method still have to be validated; for example, the importance of inter-observer variability in perceiving and encoding bite categories and how this can affect estimations of forage intake. In their experiment with cattle and goats, Bonnet et al. (2011) showed that inter-observer variability in bite-mass estimation disappeared after 5 days of training.

As with any method, continuous bite monitoring has limitations and is not adapted to all situations. The need for tame animals can limit its use with wild herbivores or dangerous animals. Night observations of biting are difficult as they involve the use of powerful flashlight that can disturb the animal. But reliable observations can be conducted without additional light.
during dawn and dusk, allowing covering the entire daylight period. This method is also time consuming in the field as an observer can follow only one animal at a time. Video recording has often been proposed as an alternative, but it cannot substitute for direct observations and rapidly becomes un-useful in complex plant communities. First, video recording does not capture a three-dimensional perspective as do human eyes, making particularly difficult estimates of plant dimensions, bite depth or position of the selected tissues within the plant, even with monospecific pastures. Second, colour and texture of plant tissues are not well captured, making it considerably more difficult to identify plant species in mixed communities. Staying by foot on the side of the animal, the observer has access to the environmental context of the local plant community. The observer can touch or smell plant tissues, which is often helpful for identifying plant species and their growth-stage.

Several non-observational techniques exist for estimating BM, bite rate or daily intake in a complex feeding environment. Automatic grazing jaw-movement recorders (e.g. Penning 1983; Rutter et al. 1997) or acoustic monitoring (Laca et al. 1999; Delagarde et al. 1999) allow to assess bite rate and, more recently, to distinguish among cropping, chewing and ruminating jaw movement, as well as combined chew bites (Laca and WallisDeVries 2000; Ungar and Rutter 2006). Thanks to recent developments in computational processing, advances have been made in the use of acoustic monitoring to estimate short-term intake rates and species selection among a limited numbers of species (Laca and WallisDeVries 2000; Milone et al. 2009; Galli et al. 2011). However, these advances are still limited to simplified and controlled swards. It could be profitable, in complex feeding environment, to combine acoustic monitoring, which gives access to the exact timing of bite events as well as the number and timing of chewing and ruminating jaw movements, with continuous bite monitoring, which gives access to BM, the nature of selected plant tissues, their location within the plant and the feeding-station behaviour. N-alkane techniques (Dove and Hayes 1991), wildly use in livestock science, are particularly valuable for estimating daily intake. They, however, rely on direct observation and hand-plucking to get representative samples of the diet. Combining continuous bite monitoring with N-alkane techniques would allow assessing daily intake as well as understanding how the animal uses the range of available resources to reach this level of intake. These methods are not antagonistic and grazing study would probably gain by combining them.

The continuous bite-monitoring method allows to examine the dynamics of herbivores’ foraging in their natural living environment and along a continuous range of scales. For example, the functional value of food items can be questioned not only as a function of their instantaneous intake rate of DM or energy, but also as a function of their spatial location within the plant and the plant community, or their temporal location within the meal. Understanding the foraging behaviours and strategies of grazing herbivores requires complementary approaches such as field observations, highly controlled experiments, and large-scale production or population-dynamic studies. However, we think that field observations need to be conducted first. Mostly because while observing animals without having any preconceived model in mind, the scientist places himself in a position to identify processes that are relevant in natural grazing conditions. Afterwards, theoretical questions can be raised and investigated in controlled experiments. Finally, the scientist can return to the field to explore how the cause–effect relations tested in controlled experiments apply in more complex situations.

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